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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 3. Parentage of *Lesbia ortoni* Lawrence

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Abstract.—*Lesbia ortoni* Lawrence, 1869, collected in the Quito Valley, Ecuador, is shown to be a hybrid between *Lesbia victoriae* and *Ramphomicron microrhynchum,* sympatric inhabitants of Andean forest edge and shrublands from Colombia to Peru. The hybrid exhibits a blended mosaic of plumage characters of the parental species. Although the parental species differ significantly in size, the external measurements of the hybrid approximate those predicted by least squares regression.

Ornithological literature of the 19th century is littered with the descriptions of dozens of enigmatic trochiline taxa from South America (Gould 1861, Salvin 1892, Boucard 1893) that now are treated as plumage mutations or hybrids (e.g., Berlioz & Jouanin 1944, Greenway 1978, Graves 1990). Unfortunately, these taxonomic disposals were often too brief and insufficiently documented to permit considered rejection of alternate hypotheses. Consequently, the status of a significant number of nominal taxa, now all but forgotten, in fact is unresolved.

The spectacular holotype of *Lesbia ortoni* Lawrence, 1869, was sent to Professor Orton of Vassar College from the Quito Valley of Ecuador (see Greenway 1978). It was deposited in the American Museum of Natural History (AMNH) on loan, 21 October 1921; ownership was finally transferred to the AMNH in March 1965 (fide M. LeCroy, pers. comm.). *Lesbia ortoni* was considered a valid species for more than 50 years (Elliot 1879, Salvin 1892, Boucard 1893, Oberholser 1902, Cory 1918, Chapman 1926). Mulsant & Verreaux (1876) erected the genus *Zodalia,* with *ortoni* as the type species. Simon (1921) treated *ortoni* as a junior synonym of *Zodalia glyceria,* believing it to represent the adult male plumage of that taxon (Peters 1945). Finally, in a terse appraisal of several puzzling taxa, Meyer de Schauensee (1947) pronounced as hybrids both *ortoni* and *Z. glyceria* (*Lesbia victoriae* × *Ramphomicron microrhynchum*). This opinion was followed implicitly by subsequent authors (e.g., Morony et al. 1975, Greenway 1978, Fjeldså & Krabbe 1990, Sibley & Monroe 1990, Collar et al. 1992). Meyer de Schauensee's proposal could be correct, but rigorous documentation of *Lesbia ortoni* is a critical and necessary first step in unraveling the parentage of other enigmatic Andean taxa believed to represent hybrids (Graves, unpubl.). Here I provide a detailed hybrid diagnosis of *Lesbia ortoni* employing the methods and assumptions outlined in Graves (1990).

Materials and Methods

The unsexed holotype of *L. ortoni* (AMNH 156651), a relaxed taxidermy mount with glass eyes, lacks the left wing (at the time of my first examination of the specimen in March 1986). The greatly elongated rectrices, large brilliant gorget, purple dorsal plumage, and unstriated maxillary ramphothecum indicate that the specimen is an adult male in definitive plumage (Figs. 1, 2). The unique appearance of *Lesbia or-*

Fig. 1. Lateral view of the type of *Lesbia ortoni* Lawrence (AMNH 156651).

toni cannot be attributed to mutation or developmental variation of any known taxon. It must then represent a hybrid or a valid taxon. As hybrids have no standing in zoological nomenclature, the burden of proof lies with the taxonomist to reject conclusively the hybrid origin of *L. ortoni* before bestowing species status on it. As the results will show, I was unable to reject the hypothesis of hybridity.

Assuming a hybrid origin of *L. ortoni,* the pool of potential parental species (=geographic pool) includes the species of hummingbirds (n = 48; see Appendix 1 in Graves 1996b) known to occur regularly above 2000 m elevation in the Ecuadorian Andes (Chapman 1926, Fjeldså & Krabbe 1990). I compared *L. ortoni* directly with males of the potential parental species and the holotype of *Chalcostigma purpureicauda* at the American Museum of Natural History (AMNH 483931). Notes, photographs, and videotape of *L. ortoni* were compared with the holotypes of *Zodalia glyceria* (The Natural History Museum, BM[NH] 1888.7.25.184), *Zodalia thaumasta* (National Museum of Natural History, Smithsonian Institution, USNM 173911), and *Heliangelus zusii* (Academy of Natural Sciences of Philadelphia, ANSP 159261; see Graves 1993a). The taxonomic status of *C. purpureicauda, Z. glyceria,* and *Z. thaumasta* will be addressed in future papers.

Color descriptions were made under natural light. Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 1). Measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

The hybrid diagnosis was approached in a hierarchical manner. The presumed parental species of *L. ortoni* were hypothesized through the comparative analysis of plumage pattern and color and feather shape. As a second step, the restrictive hypothesis was tested with the quantitative analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, 1993b, 1996a; Graves & Zusi 1990).

Results and Discussion

Characters of *Lesbia ortoni* (hereafter hybrid) that permit its parental species to be identified include: large brilliant gorget; forked tail (depth = 59.7 mm); tips of outermost rectrices "bowed" in cross section; purple feather tips on dorsal body plumage; lack of brilliant frontlet or crown; and short tibial plumes. None of the potential parental species alone exhibits this character combination.

Four species (*Ocreatus underwoodii, Lesbia victoriae, L. nuna, Aglaiocercus kingi*) in the geographic source pool have deeply forked tails. *Ocreatus* can be eliminated from consideration because the hy-

Fig. 2. Ventral view of the type of *Lesbia ortoni* Lawrence (AMNH 156651).

brid shows no evidence of racket-tipped rectrices or elongated tibial plumes. The hybrid also lacks evidence of the awl-shaped bill (dorsal profile) and brilliant crown of *Aglaiocercus kingi.* Thus, by the process of elimination, one of the "trainbearers" (*Lesbia victoriae* or *L. nuna*) is implicated in the parentage of *L. ortoni.* Plumage characters of the hybrid are consistent with this hypothesis, but it is doubtful that the specific identity of the *Lesbia* parent can be determined from plumage color or pattern alone.

Determination of the other parent seems straightforward. Only one species in the geographic pool, *Ramphomicron microrhynchum,* has the rich purple dorsal plumage (including crown) exhibited by the hybrid. In fact, the hybrid appears to exhibit a blend of definitive male plumage characters of *R. microrhynchum* and the trainbearers (*Lesbia* sp.). No other combination ($\binom{48}{2} = 1128$ possible pairs of species) of species in the geographic pool could have produced the phenotype of the hybrid (Appendix).

External measurements.—Examination of external measurements enables identifi-

Table 1.—Ranges and means (± one standard deviation) of measurements (mm) of adult male *Lesbia victoriae, Ramphomicron microrhynchum,* and the hybrid, *Lesbia victoriae* × *Ramphomicron microrhynchum* (= *Lesbia ortoni* Lawrence, 1869; AMNH 156651). Measurements of *L. nuna* are included for comparison.

	victoriae[a] (*n* = 12)	*nuna*[a] (*n* = 12)	*microrhynchum*[a] (*n* = 12)	Hybrid
Wing chord	58.7–62.2	50.3–52.8	47.3–53.5	55.8
	60.3 ± 1.1	51.8 ± 0.6	51.6 ± 1.6	
Bill length	13.5–15.3	7.5–9.0	5.9–7.0	10.1
	14.5 ± 0.6	8.2 ± 0.4	6.5 ± 0.3	
Rectrix 1	22.1–24.9	19.8–22.4	24.3–27.0	25.3
	23.5 ± 0.9	21.0 ± 0.7	26.1 ± 0.8	
Rectrix 2	26.2–31.1	25.9–28.1	28.4–34.1	31.3
	28.8 ± 1.2	27.0 ± 0.7	31.2 ± 1.4	
Rectrix 3	39.2–44.4	36.0–40.4	35.7–41.0	40.5
	42.1 ± 1.7	38.0 ± 1.4	37.7 ± 1.4	
Rectrix 4	62.1–68.5	51.3–57.6	41.5–47.3	56.1
	65.2 ± 2.3	54.3 ± 1.9	43.4 ± 1.5	
Rectrix 5	149.0–189.0	94.1–109.0	46.0–51.0	85.0
	173.7 ± 10.4	99.9 ± 4.1	48.1 ± 1.4	

[a] Collected in Ecuador.

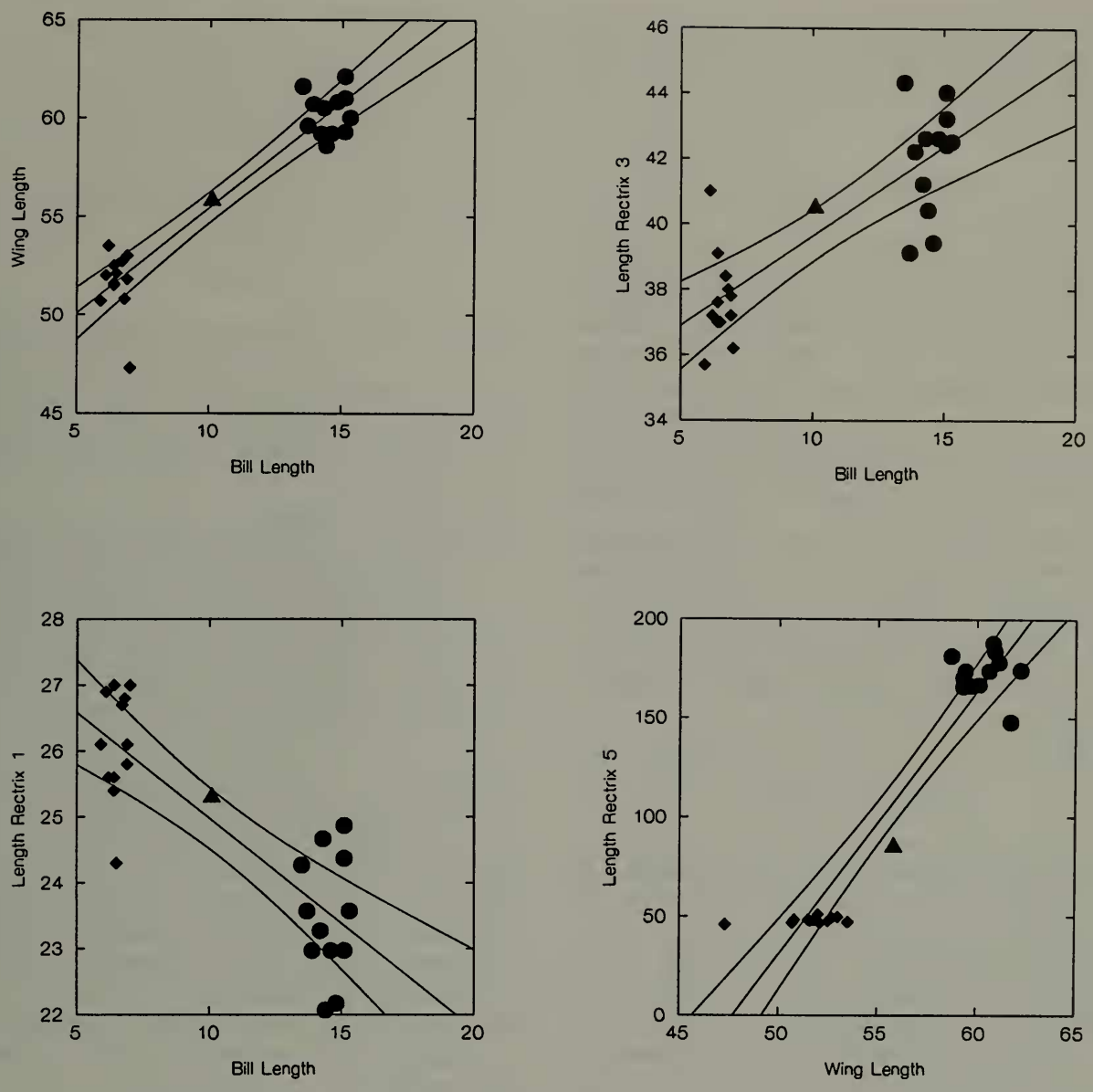

Fig. 3. Bivariate plots of mensural characters of males in definitive plumage: *Lesbia victoriae* (circles); *Ramphomicron microrhynchum* (diamonds); and their hybrid (triangle) (=*Lesbia ortoni,* AMNH 156651). Least squares regression lines and 95% confidence bands are illustrated for comparison.

cation of the *Lesbia* parent. Lengths of the hybrid's bill and wing chord exceed the cumulative range of those measurements for males of *L. nuna* and *R. microrhynchum* (Table 1). Morphological luxuriance has never been observed in trochiline hybrids; thus, *L. nuna* is not one of *L. ortoni*'s parental species. On the other hand, measurements of the hybrid fell between the character means of *R. microrhynchum* and *L. victoriae.* Of particular interest, bill and rectrix 1 measurements exhibit negative allometry in the pooled sample, whereas those of the bill and rectrix 3 show positive allometry (Fig. 3). In both cases, hybrid values approximate those predicted by the least squares regression line.

Geographic overlap.—The geographic and elevational ranges of the parental species, *Lesbia victoriae* and *Ramphomicron microrhynchum,* overlap broadly in the Andes (Fjeldså & Krabbe 1990). *Lesbia victoriae* inhabits forest edge and dry brushy slopes at 2600–4000 m elevation, whereas *R. microrhynchum* prefers cloud forest edge and paramo in more humid regions at 1700–3400 m (Graves 1985, Fjeldså & Krabbe 1990). Both species, particularly the former, are fairly common residents in the Quito region and were well represented in

19th century collections from Ecuador (Oberholser 1902, Lönnberg & Rendahl 1922, Chapman 1926).

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Appendix

General comparative description of definitive plumages of male *Lesbia victoriae, Ramphomicron microrhynchum,* and the hybrid, *L. victoriae* × *R. microrhynchum* (=*Lesbia ortoni* Lawrence, 1869; AMNH 156651). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

Dorsal feathering (capital and spinal tracts) of *victoriae* to the upper tail coverts is medium dull green; feather bases are gray and some lateral barbs are narrowly fringed with buff. These plumage areas of *microrhynchum* are deep purple; feather bases are gray separated from the purple terminal discs by a narrow greenish band.

The dorsum of the hybrid appears an amalgam of *victoriae* and *microrhynchum,* more closely resembling the latter species. The greenish subterminal band of crown and back feathers of the hybrid is wider and the purple terminal disc narrower than in *microrhynchum,* imparting a mottled purple and green appearance to the crown, hindneck and back. Scapulars are mottled green and purple; the rump and uppertail coverts of the hybrid are more uniformly purple, whereas a few feathers on the sides of the lower back are tipped with green. Purple feather tips occur ventro-laterally to the auriculars, sides of the neck, and sides of the rump.

In *victoriae,* a brilliant medium-green gorget extends from the chin to the upper breast the posterior border of the gorget is broadly lanceolate in shape. Feathers of the lores, auriculars, sides of neck, breast, and flanks are green, finely margined (10 × magnification) with buff in fresh plumage; feathers along the midline below the gorget and on the abdomen are extensively fringed with buff. Vent plumes are white; undertail coverts are buff with a muted and elongated grayish spot along the rachis; tibial plumes are buff.

The ventral color and pattern of *microrhynchum* are similar to *victoriae,* but the lores and auriculars are rich purple, the gorget more rounded and proportionally smaller. Gorget color is light green, subtly paler than in *victoriae.* Feathers of the breast and sides of *microrhynchum* are narrowly margined with grayish-buff, especially on the abdomen and along the midline below the gorget. Vent plumes in *microrhynchum* are white; undertail coverts are dark purplish brown, some tinted with green, and all broadly margined with buff or buffy–white; tibial plumes are brownish-black, narrowly tipped with buff.

The hybrid's gorget is light green, intermediate in color, size, and shape between those of the parental species. Barbs of auricular feathers are green tipped with purple. The lores are dull green with some purple reflections. The remainder of the underparts are intermediate in appearance between those of the parental species. Vent plumes are white, whereas the short tibial plumes are buff or light brown. Undertail coverts are buff with gray bases.

In *victoriae,* the rectrices (dorsally) are black with brownish-purple reflections in bright light, conspicuously (rectrices 1–4) or inconspicuously (rectrix 5) tipped with dark green. The proximal ⅓ of the lateral vane of rectrix 5 is gray (dorsally) and grayish-white (ventrally). The proximal ⅓ of the rachis (rectrix 5) is grayish–white on the ventral surface. Tips of the outermost rectrices (5) of *victoriae* are slightly subspatulate and "bowed" in cross-section. The rectrices of *microrhynchum* are black with bronzy–purple reflections, especially on rectrix 1; the rachises are blackish–brown. In cross-section, the outermost rectrices (5) are nearly flat.

The rectrices of the hybrid are intermediate between those of the parental species: (rectrix 1)—black with purplish tint proximally, shading to bronze, then coppery to coppery-purple at the tip; (rectrices 2–4)—black with bronzy reflections turning to coppery-purple at the tip; (rectrix 5)—black with faint bronzy reflections but lacking the coppery-purple tip present on the other rectrices. The lateral vane of rectrix 5 is margined dorsally with buffy–white to within 25 mm of the feather tip. Ventrally, the rachis is white or very pale buff proximally, becoming dark brownish–black near the middle of the long axis of the feather. In cross-section, rectrix 5 of the hybrid is intermediate in curvature between that shown by *victoriae* and *microrhynchum.*

Primaries and secondaries are dull dark brown in *victoriae,* and blackish-brown with purplish reflections in *microrhynchum.* The flight feathers of the hybrid are intermediate in color and iridescence. In *victoriae,* the greater wing coverts are green (same as back), the primary coverts are dark brown tipped with green, and the tiny coverts along the leading edge of the wing are green broadly edged with buff. Greater and primary coverts are blackish-brown in *microrhynchum*; the leading edge coverts are brownish-black, some narrowly margined with light brown. Wing coverts of the hybrid are intermediate in color and pattern.